# Dissociable neuroanatomical correlates of subsecond and suprasecond time perception

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# Dissociable Neuroanatomical Correlates of Subsecond and Suprasecond Time Perception

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## Abstract

■ The ability to estimate durations varies across individuals. Although previous studies have reported that individual differences in perceptual skills and cognitive capacities are reflected in brain structures, it remains unknown whether timing abilities are also reflected in the brain anatomy. Here, we show that individual differences in the ability to estimate subsecond and suprasecond durations correlate with gray matter (GM) volume in different parts of cortical and subcortical areas. Better ability to discriminate subsecond durations was associated with a larger GM volume in the bilateral anterior cerebellum, whereas better performance in estimating the suprasecond range was associated with a smaller GM volume in the inferior parietal lobule. These results indicate that regional GM volume is predictive of an individual's timing abilities. These morphological results support the notion that subsecond durations are processed in the motor system, whereas suprasecond durations are processed in the parietal cortex by utilizing the capacity of attention and working memory to keep track of time. ■

## INTRODUCTION

The ability to estimate time intervals is a fundamental skill for humans. Different ranges of time intervals are implicated in different types of perception and behavior. For instance, estimating the duration of a few hundreds of milliseconds (i.e., subsecond) is crucial for motor control (Merchant & Georgopoulos, 2006), speech perception and production (Diehl, Lotto, & Holt, 2004), music recognition, and dancing (Phillips-Silver & Trainor, 2005; Janata & Grafton, 2003), whereas estimating the duration of a few seconds (i.e., suprasecond) is involved in decision making and conscious time estimation (Buhusi & Meck, 2005; Mauk & Buonomano, 2004). Individual differences in these behaviors have been linked with the ability to explicitly estimate subsecond and suprasecond durations. For example, it has been shown that expert drummers show better performances in subsecond time reproduction task than controls (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012), and impulsive individuals have a tendency to reproduce shorter time intervals in suprasecond duration reproduction task than those who are less impulsive (Wittmann et al., 2011; Wittmann & Paulus, 2008).

Previous pharmacological studies have shown evidence of distinct neural systems for the measuring of subsecond and suprasecond intervals. It has been shown that benzodiazepines and remoxipride impair discrimination of suprasecond intervals, whereas discrimination of subsecond intervals is not influenced (Rammsayer, 1994, 1997, 1999). In contrast, ethanol impairs subsecond but not suprasecond temporal discrimination (Rammsayer & Vogel, 1992). A large body of neuroimaging studies support the idea that distinct neural systems are recruited for the measuring of subsecond and suprasecond intervals (Wiener, Turkeltaub, & Coslett, 2010; Morillon, Kell, & Giraud, 2009; Jahanshahi, Jones, Dirnberger, & Frith, 2006; Lewis & Miall, 2003a, 2006). One meta-analysis suggested that "automatic timing," in which estimation of the subsecond range is an important factor, tended to recruit the primary sensorimotor and supplementary motor cortices and the cerebellum, whereas "cognitive timing," which is associated with suprasecond timing, tended to recruit the posterior parietal and dorsolateral pFCs (DLPFCs; Lewis & Miall, 2003b, 2006).

In contrast to these consistent findings in pharmacological and neuroimaging studies, behavioral evidence for the notion of distinct neural mechanisms for subsecond and suprasecond timing is inconclusive. A recent behavioral study examined changes in coefficient variation (CV), calculated as the ratio between standard deviation (SD) and the mean of time reproduction, across a broad range of durations (from 68 msec to 16.7 min) to identify the "break point" of the time interval that may separate the neural networks involved (Lewis & Miall, 2009). The authors, however, failed to find any clear change in the CV at any point within this duration range and suggested a potential single mechanism of time estimation.

Another possible approach to determine whether the time estimations of subsecond and suprasecond intervals

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are processed by distinct neural networks is to investigate correlations between individual timing performances for subsecond and suprasecond durations and neuroanatomical data by applying a voxel-based morphometry (VBM) analysis. VBM has been successfully used to show brain structures reflecting individual differences in the perceptual skills or cognitive ability quantified by behavioral measurements (Kanai & Rees, 2011). Regarding time perception, one VBM study reported that individual anatomical differences in the primary auditory and secondary somatosensory cortices and the parahippocampal gyrus were correlated with the performance of a task involving the discrimination of durations of 12 sec, irrespective of the stimulus modalities (Gilaie-Dotan, Kanai, & Rees, 2011). This study, however, used only suprasecond durations (2 and 12 sec) for the behavioral measurements of duration discrimination performances, and it is thus unknown whether the estimations of subsecond and suprasecond durations are associated with different brain areas.

The goal of this study was to examine whether interindividual differences in brain structures correlate with the timing ability in the subsecond and suprasecond ranges. For this purpose, we used structural magnetic resonance imaging (MRI) with VBM analysis while behavioral measurements of duration discrimination thresholds were determined for subsecond (700 msec) and suprasecond (3.5 sec) durations.

## METHODS

### Participants

Forty-seven healthy, right-handed volunteers participated in the VBM study. Six participants, who showed a large change in thresholds from the first to the second block (>25% of the standard duration) either in the subsecond or suprasecond task, were excluded from data analyses. This treatment was performed because a large increase of threshold values may indicate that the participant failed to exert the same level of effort to perform the task. Data from the remaining 41 participants (22 men and 19 women, aged 19–39 years) were included in data analyses. None of the participants had a history of neurological or psychiatric illnesses. All participants gave written informed consent. This experiment was approved by the University College London Ethics Committee.

### Measurements of Duration Discrimination Thresholds

All participants performed four blocks of duration discrimination threshold measurements, two blocks for subsecond duration followed by two blocks for suprasecond duration, using visual stimuli. The visual stimulus was a white square of 3.4° against a black background presented at the center of a CRT monitor running at 100 Hz. Participants put their chin on the chin rest positioned at a distance of 57 cm from the CRT monitor. Duration discrimination thresholds were estimated by a one-up–three-down staircase procedure (Salvioni, Murray, Kalmbach, & Bueti, 2013; Bueti, Lasaponara, Cercignani, & Macaluso, 2012; Kanai, Lloyd, Bueti, & Walsh, 2011; Nagarajan, Blake, Wright, Byl, & Merzenich, 1998; Wright, Buonomano, Mahncke, & Merzenich, 1997), which converges to 79% correct performance on the psychometric function (Levitt, 1971). Participants were asked to indicate which of the two consecutively presented stimuli, separated by 1.5 sec, appeared on the screen for a longer period by pressing one of the two keys, J or K, with their right index or middle finger, respectively. The key J corresponded to "the first stimulus lasted longer"; and key K, to "the second stimulus lasted longer." Participants were also instructed not to use a counting strategy to measure the durations and to fixate their eyes at the center of the screen during the experimental session.

The standard duration was 700 msec for the subsecond task and 3.5 sec for the suprasecond task. The target (longer) stimulus had a duration of (standard duration + $T$), where $T$ was varied from trial to trial based on the one-up–three-down rule. The presentation orders of the standard and target durations were randomized across trials. For the subsecond task, the staircase started at $T$ = 300 msec, and the variable $T$ was updated by 10 msec; $T$ was decreased after three consecutive correct responses and increased after one incorrect response. Until the first reversal, 20 msec was used for fast convergence. For the suprasecond task, the staircase started at $T$ = 1 sec, and the variable $T$ was updated by 50 msec. Until the first reversal, 100 msec was used for fast convergence. The staircase procedure continued until the twelfth reversal was obtained. The average of the last six reversal points was used as the estimate of the threshold for the block. The average values of thresholds across two blocks of each task were used as the estimate of the threshold for the subsecond and suprasecond duration discriminations. The threshold values were expressed as Weber fractions (i.e., threshold $T$ divided by standard duration).

The correlation of threshold values between the first and second blocks and between the subsecond and suprasecond tasks were tested by one-tailed Pearson's correlations ($\alpha = 0.05$). The differences in the mean threshold values between the first and second blocks and between the subsecond and suprasecond tasks were tested by one-tailed paired $t$ tests ($\alpha = 0.05$).

### MRI Data Acquisition

MR images were acquired on a 1.5-T Siemens Avanto MRI scanner (Siemens Medical, Erlangen, Germany). High-resolution whole-brain MR images were obtained using a T1-weighted three-dimensional magnetization-prepared rapid acquisition gradient-echo sequence (repetition time = 2.73 sec, echo time = 3.57 msec, voxel size = 1.0 × 1.0 × 1.0 mm).

### VBM Preprocessing

Whole-brain T1-weighted MR images were first segmented for gray matter (GM) and white matter (WM) using the segmentation tools in Statistical Parametric Mapping 8 (SPM8, www.fil.ion.ucl.ac.uk/spm/). Subsequently, we performed diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL) in SPM8 for intersubject registration of the GM images (Ashburner, 2007). To ensure that regional GM volume is maintained after the registration, the registered images were modulated by the Jacobian determinant of the flow fields computed by DARTEL. The registered images were transformed to Montreal Neurological Institute (MNI) stereotactic space using affine and nonlinear spatial normalization and then smoothed with a Gaussian kernel of 10-mm FWHM.

To maximize the sensitivity of VBM in the cerebellum, we performed another VBM analysis that focused on the cerebellum using a spatially unbiased atlas template of the cerebellum and brainstem (SUIT). The preprocessing including isolation of the cerebellum, normalization into SUIT space using DARTEL engine, and reslicing were performed using the algorithms included in the SUIT toolbox version 2.7 (www.icn.ucl.ac.uk/motorcontrol/imaging/suit.htm). The images were then smoothed with a Gaussian kernel of 5-mm FWHM.

### Statistical Analysis of VBM

To control the differences in the global brain size across participants, each preprocessed data were divided by the value of the whole-brain volume (i.e., sum of total GM and WM volumes). A multiple regression analysis was performed on the smoothed GM images in SPM8. The design matrix included variables of the subsecond and suprasecond duration discrimination thresholds (i.e., Weber fractions). To minimize the possible bias of age and sex of participants, these variables were also included in the design matrix as covariates of no interest. By using this design matrix, we first explored the brain areas in which the interindividual differences in the regional GM volume correlated with the subsecond or suprasecond duration discrimination thresholds. Then, to determine whether there were any brain areas that correlated differentially to the two duration ranges, we compared the regression coefficients for the subsecond and suprasecond thresholds.

Unless otherwise noted, a statistical threshold of $p < .001$ voxel-level uncorrected and cluster size $k > 300$ were used to determine statistically significant voxels. We also report here whether the detected clusters survived even after nonstationary cluster-level correction at a threshold of $p < .05$, which corrects nonuniform smoothness in the VBM data set that affects cluster size inference. The correction was done using NS toolbox (fmri.wfubmc.edu/cms/software#NS) (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004) on SPM5. We report findings in the cerebrum based on the results of the whole-brain VBM analysis; whereas that in the cerebellum, based on the results of the cerebellar VBM analysis using SUIT.

Although SPM identifies significant clusters and their peak coordinates based on $t$ maps, which essentially show "signal-to-noise ratio," the peak coordinates of a cluster can be shifted from the actual peak of the "signal" toward a low-variance location because of a nonlinear effect of spatial smoothing on the voxel variances. To avoid this potential inaccuracy in estimating the anatomical locations of peak voxels, we used an algorithmic solution proposed by Reimold, Slifstein, Heinz, Mueller-Schauenburg, and Bares (2006). In this method, statistical assessment was initially performed on $t$ maps, but the peak coordinates are estimated from contrast images. In this procedure, significant clusters were first determined by a voxel-level threshold ($p < .001$, uncorrected). Then, the mean contrast within the cluster was computed as a new threshold value for the contrast image. Voxels contiguous to the original peak voxel in the $t$ map were included in the cluster provided that they satisfy a secondary threshold (i.e., masked contrast [primary threshold OR (contrast > regional least significant contrast AND secondary threshold)]; Reimold et al., 2006). Note that, in this approach, statistical inferences were based on traditional $t$ maps, but only the estimates of peak coordinates involved evaluation of contrast parameters. To determine the precise peak coordinates for each detected cluster, we applied this approach to our VBM analyses using MASCOI toolbox version 2.11 (homepages.uni-tuebingen.de/matthias.reimold/mascoi). The secondary threshold was set at $p < .005$, uncorrected.

The locations of the peak coordinates were labeled using SPM Anatomy toolbox version 1.8 (www.fz-juelich.de/SharedDocs/Downloads/INM/INM-1/DE/Toolbox/Toolbox_18.html; Eickhoff et al., 2005) that includes Diedrichsen's probabilistic atlas of the cerebellum (Diedrichsen, Balsters, Flavell, Cussans, & Ramnani, 2009). The correlations between GM volumes at the peaks and Weber fractions were tested by one-tailed Pearson's correlation test at a threshold of $p < .005$, which was identical to the secondary threshold described above.

## RESULTS

### Duration Discrimination Performances

We found that the Weber fractions determined for the first and second blocks were correlated both in the subsecond ($r = .527$, $p < .001$) and suprasecond ($r = .299$, $p < .05$) tasks (Figure 1A and B, left). Paired $t$ tests showed that the mean values of the Weber fractions of the first and second blocks across participants were not different in the subsecond ($t(40) = 0.959$, $p > .05$) and suprasecond ($t(40) = 0.602$, $p > .05$) tasks, confirming the reliability of the threshold measurement procedures (Figure 1A and B, right). The number of trials required to obtain the Weber

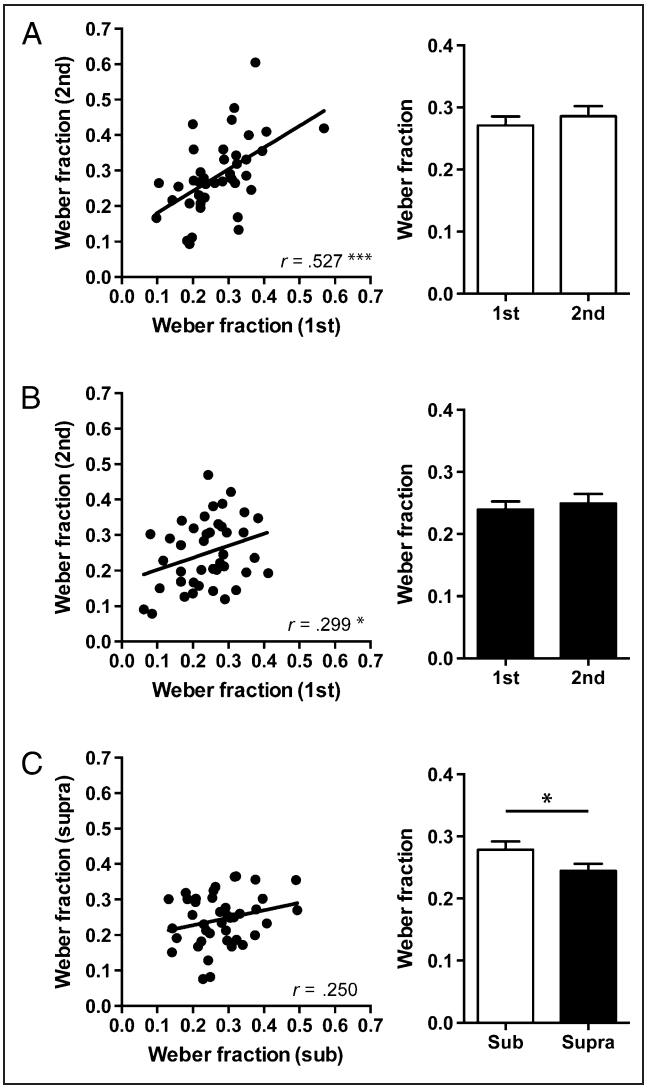


**Figure 1.** Behavioral performance. Correlation of Weber fractions between first and second blocks of (A) subsecond and (B) suprasecond tasks (left). The mean Weber fractions for each block are shown on the right. (C) Correlation of Weber fractions between subsecond and suprasecond tasks (left). Bars shown on the right indicate the mean of Weber fractions across participants. Each data point represents one participant. Error bars indicate standard errors. *$p < .05$, ***$p < .001$. 1st = first block; 2nd = second block; Sub = subsecond; Supra = suprasecond.

fractions (i.e., sum of the number of trials over the two blocks) were, on the average, 127 (range = 93–166, *SD* = 19.6) and 114 (range = 87–141, *SD* = 14.5) for the subsecond and suprasecond tasks, respectively.

The individuals' Weber fractions (i.e., means of the Weber fractions over the two blocks of measurements) were largely variable across the participants both in the range of subsecond (range = 0.132–0.494, mean = 0.279, *SD* = 0.086) and suprasecond (range = 0.076–0.365, mean = 0.244, *SD* = 0.073) durations. Importantly, interindividual differences of the Weber fractions in the subsecond and suprasecond tasks were not correlated ($r = .250$, $p > .05$; Figure 1C, left). The mean Weber fraction of the subsecond task was significantly higher than that of the suprasecond task ($t(40) = 2.237$, $p < .05$; Figure 1C, right), indicating that participants showed relatively better performances in the suprasecond than subsecond task.

### GM Volume in the Anterior Cerebellum Correlated with Subsecond Thresholds

The VBM analysis showed that individual differences of regional GM volume in the bilateral cerebellum correlated with subsecond discrimination thresholds (Figure 2A–D; Table 1). The greater GM volumes in the left anterior cerebellum (lobule VI; $r = -.496$, $p < .001$; Figure 2A–C and E, left) and the right anterior cerebellum (lobule VI; $r = -.582$, $p < .0001$; Figure 2B–D and F, left) were associated with lower subsecond discrimination thresholds. The cluster in the right cerebellum survived even at a more conservative cluster-level threshold ($p < .05$ nonstationary cluster-level corrected; Table 1). No brain regions had a significant positive correlation with the subsecond thresholds. Neither did the GM volumes in the left anterior cerebellum ($r = .313$, $p > .005$; Figure 2E, right), nor in the right anterior cerebellum ($r = .158$, $p > .005$; Figure 2F, right), nor in any other areas in the cerebellum showed a significant correlation with suprasecond thresholds.

### Parietal GM Volume Correlated with Suprasecond Thresholds

Whereas the GM volumes in the bilateral anterior cerebellum correlated with the duration discrimination threshold in the subsecond range, individual differences in discrimination thresholds in the suprasecond range correlated with the GM volume variability of the right inferior parietal lobule (IPL; Figure 3A; Table 1). The smaller regional GM volumes in the right IPL were associated with better performance in the suprasecond duration discrimination task ($r = .433$, $p < .005$; Figure 3B, right) but not with subsecond performance ($r = -.358$, $p > .005$; Figure 3B, left). None of the brain areas had a significant negative correlation with the suprasecond thresholds.

### Specificity of the Cerebellum and IPL for Subsecond and Suprasecond Performances

We examined whether any brain areas correlated differentially to the two duration ranges by comparing the regression coefficients for subsecond and suprasecond thresholds. We found that a cluster in the right IPL showed dissociation between these different duration ranges (Table 1). Note that the right IPL cluster overlapped with the area that was found to correlate with suprasecond thresholds in the earlier analysis, suggesting that the dissociation between the subsecond and suprasecond ranges in this area resulted from its strong correlation with the thresholds for the suprasecond task.

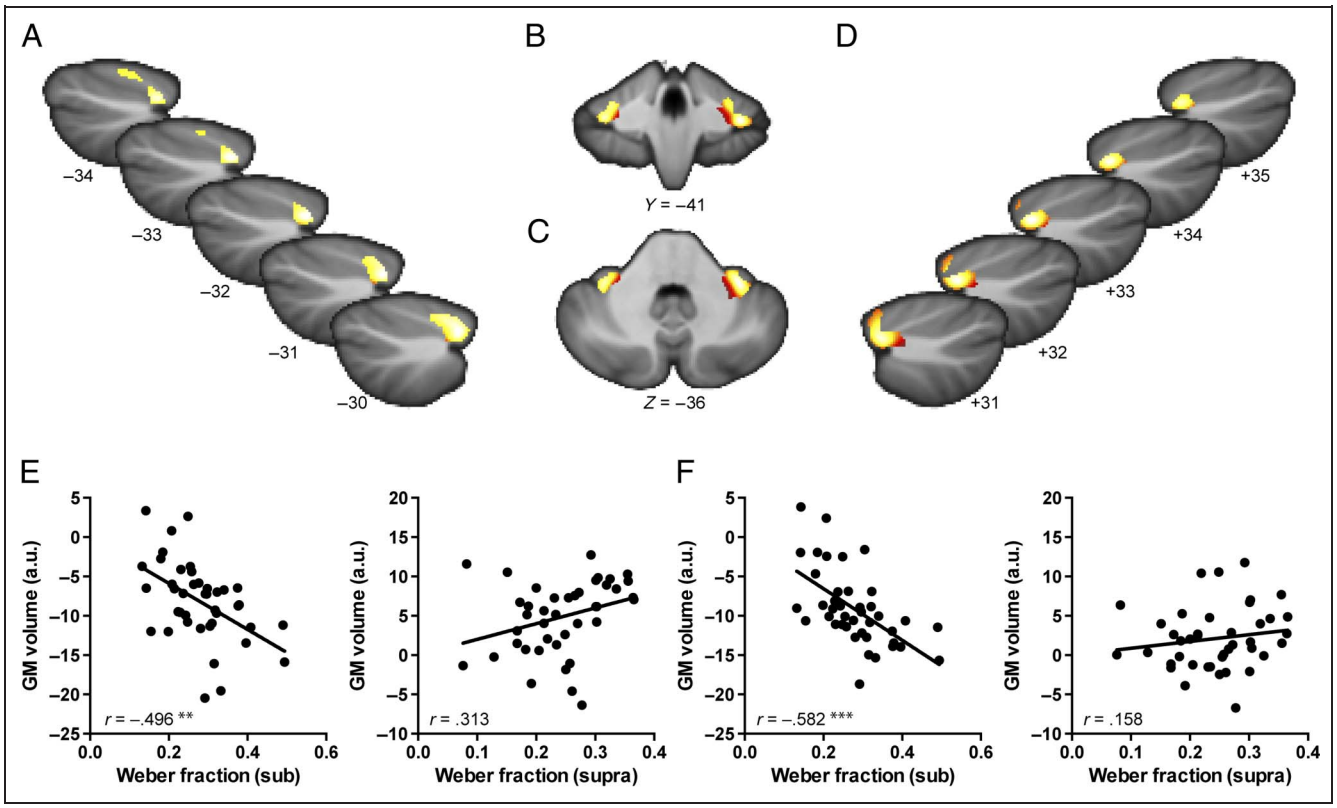


**Figure 2.** Correlation between regional GM volume in the cerebellum and subsecond discrimination thresholds. (A–D) The right and left cerebellum clusters showing significant correlations with subsecond thresholds are shown by sagittal (A and D), coronal (B), and axial (C) slices. The numbers next to each figure indicate $x$ (A and D), $y$ (B), and $z$ (C) coordinates for the slices. The blobs are superimposed on the cerebellar template in SUIT toolbox. The significant clusters are shown at the threshold of masked contrast ($p < .001$ uncorrected OR [contrast > regional least significant contrast AND $p < .005$ uncorrected]) that was used to identify the peak location of the cluster with MASCOI (see Methods for full details) for presentation purpose. Plots of the correlations between regional GM volumes and Weber fractions are shown for the peak coordinates in the left cerebellum ($x, y, z = -32, -40, -35$; E) and in the right cerebellum ($x, y, z = 33, -41, -37$; F). Within each panel, correlations with subsecond thresholds are shown on the left and with suprasecond thresholds on the right. Each data point represents one participant. $^{**}p < .001$, $^{***}p < .0001$. sub = subsecond; supra = suprasecond; a.u. = arbitrary unit.

The clusters in both the right and left anterior cerebellum were dissociated with respect to the degree of their correlations across the duration ranges when a slightly liberal cluster-level threshold was used as the significance criterion ($p < .001$ voxel-level uncorrected, cluster size $k > 0$), supporting the finding that the GM volumes in the bilateral cerebellum were specifically associated with the subsecond range.

## DISCUSSION

### Dissociation between Subsecond and Suprasecond Tasks at Behavioral Level

The behavioral data showed that participants discriminated suprasecond durations better than subsecond durations. This finding is consistent with recent behavioral data that demonstrated a continuous logarithmic decrease in CV in a time reproduction task in the range of 68 msec and 16.7 min (Lewis & Miall, 2009). The authors suggested that the results might indicate a potential single mechanism of time perception, although retaining the possibility that the apparent continuous decrease of CV might result from overlapping functions produced by multiple mechanisms. On the basis of the single mechanism hypothesis, the subsecond and suprasecond thresholds should have correlated in this study. Our behavioral result, however, showed that the threshold values did not correlate with each other, a finding that rather supports the notion that subsecond and suprasecond time estimations are mediated by distinct neural mechanisms.

### Subsecond Timing Embedded in the Motor System

The significant correlations between the subsecond threshold and regional GM volumes in the anterior cerebellum support the idea that the neural basis for subsecond time estimation is embedded in the motor system (Koch, Oliveri, & Caltagirone, 2009; Coull, Vidal, Nazarian, & Macar, 2004; Ivry & Spencer, 2004; Nobre & O'Reilly, 2004). A large number of neuroimaging studies have reported the involvement of the cerebellum in subsecond timing tasks (Hayashi et al., 2013; Wiener

**Table 1.** Anatomical Labels and Statistical Results of the VBM Analyses

| | | MNI Coordinates | | | | |
|---|---|---|---|---|---|---|
| *Cluster Size ($mm^3$)* | *$Z_{max}$ Score* | *x* | *y* | *z* | *Side* | *Location* |
| *Subsecond, Negative Correlation* | | | | | | |
| 748 | 4.11* | 33 | −41 | −37 | R | Cerebellum (VI) |
| 334 | 3.60 | −32 | −40 | −35 | L | Cerebellum (VI) |
| *Suprasecond, Positive Correlation* | | | | | | |
| 1083 | 3.43 | 58 | −33 | 45 | R | IPL (PF) |
| *Suprasecond > Subsecond* | | | | | | |
| 1252 | 3.54 | 58 | −36 | 45 | R | IPL (PF) |

L = left; R = right; MNI coordinates = the coordinates that were identified from contrast images using MASCOI toolbox.

*$p < .05$, nonstationary corrected at cluster level.

et al., 2010; Bueti, Walsh, Frith, & Rees, 2008; Lewis & Miall, 2003a, 2006; Jantzen, Steinberg, & Kelso, 2005; Lewis, Wing, Pope, Praamstra, & Miall, 2004; Schubotz, Friederici, & von Cramon, 2000; Penhune, Zattore, & Evans, 1998). A meta-analysis suggested that the activation of the cerebellum was independent of the nature of tasks involving either motor or perceptual timing (Wiener et al., 2010).

A number of TMS studies have demonstrated causal involvement of the bilateral (Koch et al., 2007) or right cerebellum (Del Olmo, Cheeran, Koch, & Rothwell, 2007; Fierro et al., 2007; Lee et al., 2007) in subsecond timing tasks. For instance, Koch et al. (2007) applied repetitive off-line TMS to the left cerebellum and the right DLPFC and measured the participants' time reproduction performances in the range of around 500 msec and 2 sec (Koch et al., 2007). Their results showed that TMS over the left cerebellum impaired performance of subsecond but not suprasecond time estimation, whereas the right DLPFC impaired only suprasecond timing. Their second experiment showed that TMS impaired the performance in the subsecond range when it was applied to the left and right cerebellum during the encoding of time intervals but not when it was applied during the period of reproduction, suggesting that the cerebellum plays an important role in the encoding of subsecond durations.

Although these previous studies have consistently reported the involvement of the cerebellum in the estimation of subsecond durations, the relationship with each subregion is less clear. Whereas the present VBM study demonstrated that the GM volumes in the anterior part of the cerebellum correlated with subsecond duration discrimination performances, a meta-analysis of fMRI studies showed that activation in the cerebellum was most commonly found in the posterior part of bilateral cerebellum during subsecond timing tasks (Wiener et al., 2010). A lesion study reported that time reproduction in the subsecond range was impaired in patients with damage involving the middle- to superior-cerebellar lobules (Harrington, Lee, Boyd, Rapcsak, & Knight, 2004). TMS studies suggest that the involvement of lateral or medial

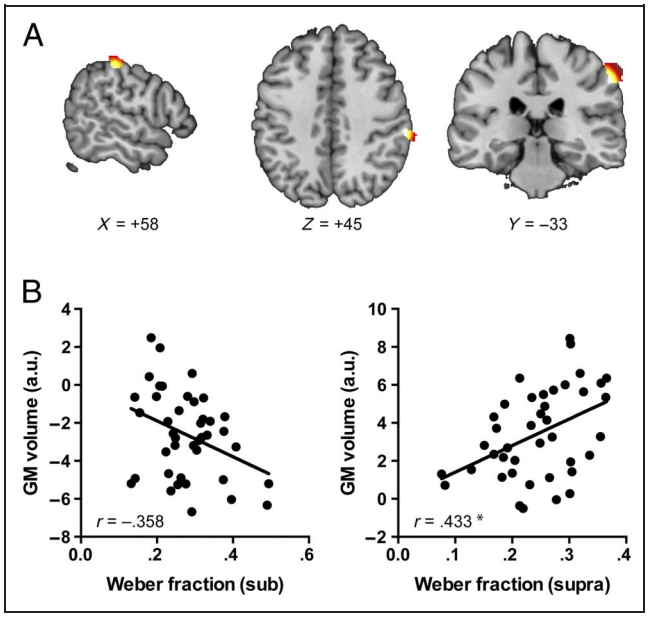


**Figure 3.** Correlation between regional GM volume in the parietal cortex and suprasecond discrimination thresholds. (A) The right IPL cluster showing a significant correlation with suprasecond thresholds is shown by sagittal (left), axial (center), and coronal (right) slices. (B) Plots of the relationship between GM volumes and Weber fractions for subsecond (left) and suprasecond (right) tasks at the peak of the right IPL cluster ($x, y, z = 58, -33, 45$). The blobs were superimposed on the normalized colin27 image. The significant clusters are shown at the threshold of masked contrast ($p < .001$ uncorrected OR [contrast > regional least significant contrast AND $p < .005$ uncorrected]) that was used to identify the peak location of the cluster with MASCOI (see Methods for full details) for presentation purpose. Each data point represents one participant. *$p < .005$. sub = subsecond; supra = suprasecond; a.u. = arbitrary unit.

regions might depend on the stimulus modalities (Coull, Cheng, & Meck, 2011; Del Olmo et al., 2007; Theoret, Haque, & Pascual-Leone, 2001). Further studies are needed to elucidate the source of this variability, which could result from differences in methodology, the nature of the tasks (e.g., motor timing vs. perceptual timing), task goals (e.g., explicit vs. implicit timing), and the stimulus modalities of the temporal cues.

### Suprasecond Timing and Parietal Region

The association of the IPL with estimation of suprasecond intervals is highly consistent with previous neuroimaging studies that showed stronger involvement of the IPL in suprasecond than subsecond timing tasks (Morillon et al., 2009; Jahanshahi et al., 2006). Moreover, the involvement of the IPL is in line with the idea that suprasecond time estimation is mediated by attention and working memory (Lewis & Miall, 2006). In pharmacological studies, it has been shown that benzodiazepines and remoxipride that influence working memory impair suprasecond time perception without affecting subsecond timing (Rammsayer, Hennig, Haag, & Lange, 2001; Rammsayer, 1994, 1997, 1999; Rammsayer & Vogel, 1992). Similar dissociation was also shown by the administration of selective noradrenaline reuptake inhibitor reboxetene (Rammsayer et al., 2001). In an fMRI study, the IPL activity during suprasecond time estimation was explained by the higher demand on attention to track long intervals (Macar et al., 2002). The relationship between individual differences in the attention capacity and parietal structure could be supported by a recent VBM study showing a correlation between interindividual differences in distractibility and parietal regional GM volume (Kanai, Dong, Bahrami, & Rees, 2011). Interestingly, the authors found that smaller distractibility scores were associated with smaller parietal GM volumes, which is in line with our finding that better suprasecond timing ability was associated with a smaller GM volume in the parietal cortex. Therefore, our results suggest that better ability to estimate suprasecond time intervals is supported by better ability to focus attention on a specific stimulus feature (i.e., duration) and to keep temporal information in working memory and that these abilities are reflected in the small GM volume in the parietal cortex. Future VBM studies on timing ability together with psychological measures of working memory and attention capacity will provide further insight into whether individual differences in the GM volume in the IPL are specifically associated with suprasecond timing ability.

### Previous Neuroanatomical Studies on Time Perception

To our knowledge, two earlier studies have investigated the relationship between structural differences of the brain and duration discrimination abilities. A study by Bueti et al. (2012) showed that training to discriminate durations in the subsecond range with visual stimuli led to improvement in the performance and structural changes in the occipital and parietal cortices, insula, and cerebellar lobule VIIa-crus1 (Bueti et al., 2012). Our results may appear at odds with these findings, as we did not find structural correlates with the subsecond range in those brain regions. One potential explanation is that we examined individual differences in a cross-sectional design, whereas Bueti et al. (2012) observed longitudinal structural changes induced by training. It is possible that different neural structures are highlighted by naturally occurring individual differences and changes because of training.

Whereas Bueti et al. (2012) investigated the effect of training on anatomical structure in the subsecond range, another VBM study of time perception by Gilaie-Dotan et al. (2011) investigated associations between suprasecond duration discrimination performance and regional GM volume in a cross-sectional design (Gilaie-Dotan et al., 2011). In this study, the authors measured duration discrimination performance using standard durations of 2 and 12 sec by presenting the stimulus either in the visual or auditory modality. Whereas the auditory duration discrimination performance of the 2-sec standard duration was found to correlate with the GM volume of the primary visual cortex, no correlation was found for the performance of the 2-sec visual duration discrimination anywhere in the brain, although this condition (i.e., 2-sec standard visual stimulus) was the closest condition to our suprasecond task using 3.5-sec visual stimuli as the standard. One possible explanation for the lack of correlation between anatomical structure and the 2-sec visual duration discrimination performance in the Gilaie-Dotan's study might be because of a floor effect in the behavioral performance. The most important contribution of our study is that, whereas Gilaie-Dotan's study showed the neuroanatomical correlates of suprasecond (2 and 12 sec) task performances across different modalities, we showed distinct anatomical structures associated with the perception of subsecond and suprasecond durations.

### Positive versus Negative Correlations

We found that better performance was not always associated with larger regional GM volumes but that the size–performance relationship depended on the region. Whereas it is often assumed that greater GM volume is associated with better behavioral performance, there are several studies reporting an opposite relationship, for example, in congenital amusia (Sowell et al., 2004; Sowell, Thompson, Tessner, & Toga, 2001). One potential explanation for "the smaller the better" relationship might be provided by efficient synaptic connections, as in the neural pruning process taking place during the maturation of the brain (Kanai & Rees, 2011). In the course of development, the pruning of weak synapses results in reduction of cortical GM volume and can improve processing efficiency (Gogtay et al., 2004). Although the

relationship between structural volume and functional performance remains an open question, systematic associations between structure in the IPL and cerebellum and behavioral performances regardless of the direction of the association imply the relevance of these regions in the timing tasks.

## Conclusion

In this study, we showed that interindividual differences in the regional GM volume were predictive of an individual's ability to estimate durations. Different brain areas were associated with the ability to discriminate subsecond and suprasecond intervals. The bilateral anterior cerebellum was implicated in subsecond timing, in line with the idea that the cerebellum is crucial for time estimation in the subsecond range. The specific association of the right IPL with suprasecond durations may suggest that the capacity of attention and working memory supports time estimation in the suprasecond range. Our study provides neuroanatomical evidence of distinct neural systems for subsecond and suprasecond time estimations.


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